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Impacts of abiotic and biotic factors on terrestrial leeches in Indonesian Borneo

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1. ABSTRACT PAGE

Haemadipsid leeches are ubiquitous inhabitants of tropical and sub-tropical forests in the Indo-Pacific region. They are increasingly used as indicator taxa for biomonitoring, yet very little is known about their basic ecology. For example, to date no study has assessed the occurrence and distribution of haemadipsid leeches across naturally occurring gradients within intact habitats. We analysed a long-term data set (2012-2020) on the closely related tiger (*Haemadipsa picta*) and brown (*Haemadipsa spp.*) leech species to investigate if and how abiotic and biotic factors influence their occurrence across a gradient of forest types at an undisturbed tropical rainforest site in Indonesian Borneo. We compared a series of negative binomial mixed models and found that, of the abiotic factors, soil moisture had the largest positive effect on encounter rates of both leech species. Among biotic factors, forest type had differential effects on counts of the two species: while tiger leech counts were greater in low elevation forest types, brown leech counts were greater in high elevation forest types. Additionally, we found that the presence of one species had a positive effect on the presence of the other species. Finally, our results show that the tiger leech has a narrower distribution, being restricted to lower elevation forest types with higher water retention, suggesting that the tiger leech could be more sensitive to lower soil moisture levels.

Second Abstract (Bahasa Indonesia)

Pacet haemadipsid adalah penghuni hutan tropis dan sub-tropis, yang hidup di kawasan Indo-Pasifik. Mereka seringkali digunakan sebagai taksa indikator untuk biomonitoring, namun sangat sedikit yang diketahui tentang ekologi dasar mereka. Sebagai contoh, sampai saat ini tidak ada

penelitian yang menilai keberadaan dan distribusi pacet haemadipsid di seluruh gradien alami di dalam habitat yang masih utuh. Kami telah menganalisis dari kumpulan data jangka panjang (2012-2020) tentang spesies pacet harimau (*Haemadipsa picta*) dan coklat (*Haemadipsa* spp.) yang memiliki kekerabatan dekat, untuk menyelidiki apakah dan bagaimana faktor abiotik dan biotik dapat memengaruhi kemunculannya di seluruh gradien tipe hutan pada suatu lokasi hutan hujan tropis yang tidak terganggu di Kalimantan, Indonesia. Kami membandingkan serangkaian model campuran binomial negatif dan menemukan bahwa, dari faktor abiotik, kelembaban tanah memiliki efek positif terbesar pada tingkat pertemuan kedua spesies pacet tersebut. Di antara faktor-faktor biotik, tipe hutan memiliki pengaruh yang berbeda terhadap jumlah kedua spesies: saat jumlah pacet harimau ditemukan lebih besar di tipe hutan dengan elevasi rendah, sedangkan jumlah pacet coklat ditemukan lebih besar di tipe hutan dengan elevasi tinggi. Selain itu, kami menemukan bahwa keberadaan satu spesies memiliki efek positif pada keberadaan spesies lainnya. Pada akhirnya, hasil kami menunjukkan bahwa pacet harimau memiliki distribusi yang lebih sempit, terbatas pada tipe hutan elevasi yang lebih rendah dengan retensi air yang lebih tinggi. Hasil lain juga menunjukkan bahwa pacet harimau bisa lebih sensitif terhadap tingkat kelembaban tanah yang lebih rendah.

2. KEYWORDS

3. TEXT

1. INTRODUCTION

Studying wildlife in dense tropical forests is often difficult, and researchers benefit from having a broad toolkit available to them for monitoring these populations. Along with well-established tools such as camera traps and faecal samples, the use of indicator species has emerged as a viable technique to gain insight into the distributions of tropical vertebrates (Drinkwater et al., 2019). Jawed land leeches, from the annelid family Haemadipsidae in particular, are gaining traction as model taxa for biodiversity assessments. The family encompasses over 80% of land leech species, including the species-rich genus *Haemadipsa* (Gąsiorek & Różycka, 2017; Fahmy et al., 2019). *Haemadipsa* species have recently featured in several studies that have used invertebrate-derived DNA (iDNA) as a tool to survey wildlife populations and detect presence of pathogens in wildlife populations (Schnell et al., 2012; Schnell et al., 2015; Drinkwater et al., 2018; Tessler et al., 2018; Weiskopf et al., 2018; Abrams et al., 2019; Fahmy et al., 2019; Siddall et al., 2019; Alfano et al., 2020; Drinkwater et al., 2020; Baker et al., 2021). Other work has investigated the role of leeches as vectors of animal and human pathogens (Kang et al., 2016). Despite this and their abundance across tropical ecosystems, little is known about their basic ecology. A more complete understanding of leech ecology promises to maximize the utility of these emerging techniques. For example, characterization of the distribution of leeches across natural habitat gradients can place the results of studies in disturbed systems in appropriate context.

Early research on *Haemadipsa* leeches focused primarily on their taxonomy, anatomy, and natural history, providing only simple characterizations of their geographic distribution and ecology (Moore, 1929; Smythies, 1959; Mann, 1962; Sawyer, 1981). One exception was Fogden and Proctor's (1985) experimental work which demonstrated that *Haemadipsa* species (*H. picta,* the tiger leech, and *H. zeylanica,* from the brown leech species complex) could survive several months provided humidity levels were kept high (Fogden & Proctor, 1985). Based on their findings the authors predicted that *Haemadipsa* species would likely be absent from habitats with lower humidity, such as logged forests.

Only recently have empirical studies begun to shed light on the ecology of *Haemadipsa* species. Kendall (2012) investigated changes in the occurrence of *H. picta* and *H. zeylanica* in response to abiotic factors and habitat modifications. Results showed that overall leech encounter rates dropped with rising temperature and increased with higher soil moisture, although leeches were absent from sites that had standing water. Contrary to Fogden and Proctor's (1985) predictions, Kendall (2012) found that overall encounter rates were higher in logged forests than in primary forests, but encounter rates fell to zero in oil-palm plantations. The higher overall encounter rates in logged habitats were solely due to a significant increase in *H. picta* encounter rates in logged forests. In addition, while overall encounter rates dropped with decreasing humidity, those of *H. picta* increased as humidity declined, suggesting that changing humidity affected the two leech species differently (Kendall, 2012).

Within degraded habitats, habitat structure and microclimatic conditions affected presence of *Haemadipsa* species differently (Drinkwater et al., 2019). Forests with a higher canopy and possibly more humid microclimates (Jucker et al., 2018) had a small positive effect on occupancy of *H. picta* in the wet and dry seasons (Drinkwater et al., 2019). However, such an

association was only seen in the wet season for *H. sumatrana* (of the brown leech species complex) while increasing canopy height had no effect on occupancy in the dry season. Further, *H. sumatrana* was less likely to occur in a heterogenous habitat or heavily degraded forest during the dry season, suggesting that both microclimate and habitat quality influence presence of *H. sumatrana* (Drinkwater et al., 2019).

Additionally, in a study on foraging behaviour, Gąsiorek and Różycka (2017) showed that *H. picta* used a wider range of microhabitats than *H. subagilis* (of the brown leech species complex). Specifically, *H. picta* aggregated along trails more than *H. subagilis*, where they hunted along the ground and by climbing onto vegetation thereby increasing the number and types of potential hosts. In contrast, *H. subagilis* used a more specialized habitat, preferring to hunt in leaf litter (Gąsiorek & Różycka, 2017). This preference of the brown leech species for the ground and the tiger leech for bushes has also been noted in some of the earlier work on leech fauna of Borneo (Smythies, 1959).

To date, no long-term empirical work has investigated the occurrence of different *Haemadipsa* species in different habitat types along an elevational gradient, nor across an undisturbed forested landscape. Such information is critical to understand how different *Haemadipsa* species respond to both abiotic and biotic factors within intact habitats. This is especially important given that *Haemadipsa* species are increasingly being used for biomonitoring and knowledge on their habitat preferences is critical to avoid biases (Drinkwater et al., 2019; Baker et al., 2021).

The Cabang Panti Research Site (CPRS) in West Kalimantan, Borneo, spans an elevation gradient ranging from 5 to 1100 m a.s.l. and covers seven distinct forest types (Marshall et al., 2021). As such, it is an ideal site to investigate the role of abiotic and biotic factors in

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determining distribution patterns of local *Haemadipsa* species. CPRS is home to at least two species of terrestrial leeches: *H. picta* (hereafter tiger leech) and *H. spp.,* from the brown leech species complex (hereafter brown leech), both of which we studied across the gradient of natural forest types for eight year(s). While there is no confusion pertaining to the taxonomic identification of the tiger leech, it is not possible to distinguish among brown leech species using morphological information alone. As we do not have the molecular evidence to confidently identify the brown leech species in our study area, we limit identification to the genus level. Tiger leeches and brown leeches have distinct morphological and behavioral characteristics that allow us to tell them apart in the field. The tiger leech features prominent yellow stripes and is known for a notable bite, while brown leeches have a uniformly brown colour and painless bite (Figure 1). In this study, we investigate ecological factors determining counts of the tiger leech and the brown leech, using eight year(s) of data collected across seven forest types during 14 vertebrate census surveys and a total sampled distance of 7,748.7 km (Table 1). Specifically, we investigate whether and how counts of *Haemadipsa* species are influenced by (a) abiotic factors (altitude, soil moisture, and rainfall history), and (b) biotic factors (forest type and abundance of the other leech species).

2. METHODS

1. Study site.

We gathered data at CPRS in Gunung Palung National Park, West Kalimantan, Indonesia (1°13′ S, 110°7′ E) (Figure 2). The site encompasses an area of 34 km^2 with seven distinct, contiguous

forest types that differ in geology, drainage, elevation, plant species composition, forest structure, and plant phenology (Marshall et al., 2021). These forest types are (a) peat swamp on nutrient-poor, bleached white soils overlain by variable amounts of organic matter (5 to 10 m a.s.l.); (b) freshwater swamp on nutrient-rich, seasonally flooded, poorly drained gleyic soils (5 to 10 m a.s.l.); (c) alluvial bench on rich sandstone-derived soils recently deposited from upstream sandstone and granite parent material (5 to 50 m a.s.l.); (d) lowland sandstone on well-drained sandstone-derived soils with a high clay content and sparse patches of shale (20 to 200 m a.s.l.); (e) lowland granite on well-drained, granite-derived soils (200 to 400 m a.s.l.); (f) upland granite on well-drained, granite-derived soils (350 to 800 m a.s.l.); and (g) montane on largely granite-derived soils (750 to 1100 m a.s.l.).

2. Field methods.

In 2000, AJM established a series of 14 vertebrate survey transects across the seven primary forest types at CPRS (Marshall et al., 2021) (Figure 2). The mean length of survey transects was 3.4 ± SD 0.24 km. Some transects were contained entirely in a single forest type, and others spanned multiple forest types. For analysis, transects were divided into segments that were restricted to a single forest type and varied in length from 50 to 550 m. We measured the altitude of each forest type at its approximate midpoint using a Suunto Vector Altimeter (Marshall et al., 2014). The total distance walked within each forest type per sampling occasion and for the entire duration of this study are listed in Table 1.

From November 2012 to September 2020, we systematically counted leeches along these vertebrate transects. We walked each transect at a constant, slow speed (~1 km per hour) twice

per month (starting at opposite ends), beginning at 0530 h. Surveys were normally carried out by a single observer, although occasionally two observers would walk the same transect (e.g., when new staff were trained). Every 500 m along transects or at the beginning of each segment, observers paused to examine themselves thoroughly for a period of two minutes. Any leeches attached to their bodies were counted, identified, and removed. When two surveyors were present, both individuals searched for and counted leeches, and the recorded number of leeches was combined for the two observers.

In addition to leech species and counts, within each segment, observers made a note of soil moisture and rainfall history. For soil moisture, observers examined the dampness of soil and categorized it as "wet", "moist" or "dry". They categorized rainfall history for the whole survey day as "Raining now", "Rained last night", "Rained yesterday", "Rained day before yesterday" or "Rained over 48 hours ago" based on conditions at the research station. Rainfall can sometimes be highly localized at our site, so it is possible that occasionally a segment's rainfall history assessment based on conditions at the research station may have been inaccurate. We have no reason to believe such rare mischaracterizations were biased in any particular direction, however.

3. Data analysis.

We conducted preliminary data exploration and subsequent analysis in program R (R Core Team, 2020; RStudio Team, 2021). Histograms showed that species-specific leech counts were over-dispersed, indicating that the negative binomial would be an appropriate distribution on which to base our models (Figure S1). Next, we checked for observer bias by comparing total

leech counts per observer / per km of transect; one observer (JK) consistently counted a higher number of leeches than other observers, indicating that an effect for observer was warranted in our models (Figure S2). Although most of our leech count segments were 500 m long, there was some variation in segment length (e.g., halting a leech segment before 500 m due to a change in forest type on the transect). We therefore next checked to see if segment length influenced leech counts per species (Figure S3). Leech counts were not influenced by segment length, indicating that other habitat-specific variables were perhaps driving counts (Figure S4). Finally, we plotted leech counts per species by forest type, soil moisture, rainfall histories and altitude (Figures S5-S8). All four ecological predictors appeared to influence leech counts for both species, and they were thus included in our candidate models.

To understand which abiotic and/or biotic variables were reliable predictors of leech counts of each species, we ran negative binomial mixed models using function GLMER from the Lme4 Package (version 1.1.26; R Core Team, 2020), with the following predictors - altitude, humidity, rain history, counts of the other leech species and forest type as fixed effects. We included segment ID as a random effect to account for pseudo-replication as each segment, our unit of analysis, is repeated multiple times. Some of our models, including the top models, produced non-convergence warnings, perhaps due to the large number of levels for segment ID (n = 197). Nevertheless, these models did produce interpretable and plausible estimates of effect sizes and standard errors. To confirm these results, we reran our top models without random effects. These simpler models did not produce convergence warnings and produced results that were comparable to our multi-level models (Figure S9). We therefore feel confident presenting and basing inferences on the multi-level models, which we deem preferable because they permit us to control for repeated sampling of segments.

To parse if leech species were spatially partitioned as a result of competition or forest type, we reran the best model first without counts of other leech species as a predictor and again without forest type as a predictor. We compared models with Akaike Information Criterion (AIC) (Table S1 a and b) and used Base R (R Core Team, 2020) to visualize effect sizes of predictors in the best model for each leech species (Figure S11). We considered predictors to be reliable when the 95% confidence intervals of their effect sizes did not overlap zero.

Prior to model fitting, we examined pair-wise correlation plots (Figure S10) to ensure highly correlated variables (which we define as $r > 0.75$) were not included in the same model to avoid issues with model convergence. Thus, forest type and altitude were not included together in any model. All continuous predictors (altitude and other leech species) were centered on the mean and standardized to permit direct comparison of effect size magnitude. Finally, prior to model fitting, we set "peat swamp", "dry", and "rained over 48 hours ago" as the reference levels for their respective categorical predictors.

3. RESULTS

Of the 58 negative binomial mixed models, the model with soil moisture, rain history, other leech species, forest type and observer (coded as JK or Rest) as predictor variables emerged as the best model with essentially all of the model weight (Akaike weight $= 1$) for each leech species (Table S1 a and b). For the tiger leech, except for the three highest elevation forest types, all predictors had a reliably positive effect on counts. For the brown leech, all predictors had a positive effect on counts, although not all were reliable (Figure 3). The effect sizes presented

below are back-transformed (exponentiated) beta coefficients to facilitate interpretation on the natural scale.

1. Abiotic factors.

Soil moisture had a positive effect on tiger leech counts, with the odds of counting a tiger leech increasing 4.99 (±1.08 SE) and 4.20 (±1.08 SE) fold in wet and moist conditions respectively, compared to dry conditions (Figure 3). Similarly, there was a positive effect on brown leech counts when the soil was wet and moist, with the odds of counting a brown leech increasing by 5.62 (±1.09 SE) and 3.85 (±1.09 SE) times respectively when compared to dry conditions (Figure 3). The odds of counting a tiger leech increased by 2.10 (±1.06 SE) and 1.96 (±1.06 SE) times when it had rained the previous night and the previous day respectively, when compared to when it had rained over 48 hours ago (Figure 3). Similarly, the odds of counting a brown leech increased by 1.87 (±1.08 SE) and 1.72 (±1.08 SE) times when it had rained the previous night and the previous day respectively, when compared to when it had rained over 48 hours ago (Figure 3).

2. Biotic factors.

Freshwater swamp and alluvial bench forest types have a positive effect on tiger leech occurrence, with the odds of counting a tiger leech increasing by 3.32 (±1.25 SE) and 3.29 (±1.23 SE) times respectively when compared to peat swamp, the reference level (Figure 3). In contrast, lowland granite, montane and upland granite forest types had a reliably negative effect

on tiger leech counts, with the odds decreasing by 0.27 (±1.24 SE), 0.22 (±1.30 SE) and 0.13 (±1.23 SE) times respectively, when compared to peat swamp habitat (Figure 3). Further, for every additional brown leech counted on a segment, the odds of counting a tiger leech increased by 1.21 (±1.04 SE) times (Figure 3). The brown leech had a wider distribution than the tiger leech, but counts were highest in higher elevation forest types, with the odds of counting a brown leech increasing by 34.72 (±1.23 SE) and 5.09 (±1.19 SE) times in montane and upland granite forest types respectively, when compared to the peat swamp (Figure 3). Again, for every count of a tiger leech the odds of counting a brown leech increased by 1.58 (±1.04 SE) times (Figure 3).

3. Spatial partitioning.

To assess if leech species were spatially partitioned due to competition or changing forest type, we reran the abovementioned best model, first without counts of other leech species as a predictor, and again without forest type as a predictor. The model that included forest type but excluded counts of other leech species came up as the best model for both leech species with an Akaike weight of 1 (Figure S11). The analysis shows that tiger leech counts are highest in low-lying forested habitats, whereas the brown leech had a wider distribution than the tiger leech, but counts are highest in higher elevation forest types (Figure 4).

4. DISCUSSION

We investigated the occurrence of two leech species, the tiger and brown leech, over eight year(s) across a habitat and elevational gradient to parse how abiotic and biotic factors influence

their counts. We found that the most important predictors of counts for both species were soil moisture, rainfall history, forest type, and counts of the other leech species. Despite similarities in the direction and size of effect of abiotic factors on counts, biotic factors, specifically forest type, had differential effects on counts of the two species. The tiger leech was counted more often at low elevation forest types like freshwater swamp and alluvial bench, while the brown leech was more frequently counted in high elevation forest types, such as montane forest.

Our findings are consistent with earlier work that suggested wet and humid conditions are important for terrestrial leech species (Fogden & Proctor, 1985; Enguang, 2001; Sket & Trontelj, 2008). We demonstrate that soil moisture, specifically wet and moist soil conditions, had a larger positive effect on counts of both the tiger and brown leech than recent events of rainfall. When controlling for soil moisture, rainfall within the last 48 hours still had a positive albeit a smaller effect on species counts. Prior to our assessment, few studies have empirically studied the effect of abiotic factors on leech occurrence and activity. *H. hainana* studied in rubber plantations in China were found to be less abundant in the dry season and precipitation was found to be an important predictor of their abundance (Enguang, 2001; Enguang & Chuanjing, 2000). Rubber plantations are characterized by higher light intensity, lower humidity and higher temperatures when compared to regenerating forest and primary forest habitats (Hidayat et al., 2018).

Measures of soil moisture, as opposed to current/recent rainfall conditions, may better capture the influence of soil properties such as water retention and drainage. Higher elevation forest types at CPRS are characterized by well-drained sandstone and granite-derived soils, while soils of the lowland forests generally retain more water and some experience periodic flooding (Marshall et al., 2009; Marshall et al., 2014). Our study showed that the tiger leech had a narrower distribution and was mainly restricted to low elevation forest types, while the brown

leech had a wider distribution that overlapped the distribution of the tiger leech, but counts were significantly higher in higher elevation forest types. This observation, paired with the model results showing wet and moist soil conditions as the top two predictors of tiger leech counts, suggests that the tiger leech may be more sensitive to fluctuations in soil moisture than the brown leech, and perhaps largely limited to forest soils with high water retention.

While Kendall (2012) found that encounter rates of the brown leech (*H. zeylanica*) decreased with increasing temperature, lower humidity, and lower soil moisture, these abiotic factors had the opposite effect on the tiger leech. One possible explanation for the opposite effect found in our two studies is that Kendall's (2012) took place in disturbed habitats. To explain the higher encounter rates of tiger leeches in disturbed habitats with lower soil moisture, Kendall (2012) suggested that the denser understorey in disturbed habitats creates newer niches for occupation for the tiger leech, which is known to inhabit ground vegetation, in contrast to the brown leech (*H. zeylanica*) that lives in the leaf litter. Similarly, Gąsiorek & Różycka (2017) and Drinkwater et al. (2019) found that when compared to the tiger leech, brown leech species (*H. subagilis* and *H. sumatrana*) were more sensitive to changing microclimatic conditions, specifically lower humidity. Research from other sites in Borneo have also noted differential impacts of abiotic factors on closely related invertebrate species (Luke et al., 2014; Boyle et al., 2021).

Our findings highlight an absence of competition between the two species: the presence of one was a positive predictor of the other in models that accounted for forest type. While tiger leeches are most abundant in lowland forests and counts of brown leeches were highest in higher elevation forests, the overlap in their occurrence suggests that, despite specializing in different habitats, the two may avoid inter- and intra-specific competition by exhibiting distinct

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behaviours. A previous study showed that interspecific competition was reduced in areas where tiger and brown (*H. subagilis*) leech species overlapped via horizontal and vertical partitioning (Gąsiorek & Różycka, 2017). Tiger leeches were seen aggregating closer to trails when compared to off-trail locations (Gąsiorek & Różycka, 2017). Further, the tiger leech distributed itself vertically by climbing on ground vegetation to hunt, thereby potentially accessing different host species, when compared to the brown leech (*H. subagilis*) that preferred to hunt from leaf litter (Gąsiorek & Różycka, 2017). Avoidance of intra-specific competition via temporal and spatial partitioning was noted in the case of tiger leeches (Gąsiorek & Różycka, 2017; Miler et al., 2019) but not in the case of brown leeches (*H. subagilis*) (Gąsiorek & Różycka, 2017). Larger individuals hunted from higher ambush locations in the ground vegetation (Gąsiorek & Różycka, 2017; Miler et al., 2019). Further, larger individuals were preferentially seen hunting during the morning, whereas juveniles were active throughout the day (Gąsiorek & Różycka, 2017). In order to identify how leeches at CPRS and other sites avoid competition, future research should focus on small scale differences in temporal and spatial behaviour.

Although our study offers greater resolution on leech ecology than previously available, our findings have several limitations. First, our researchers only collected data at particular times, from 0530 to 1130 h, and therefore our dataset could not capture diurnal variation in leech detectability (Gąsiorek & Różycka, 2017). As mentioned above, research has described intra- but not interspecies differences in feeding times, so this potential confound merits further exploration. The second limitation is that our leech counts do not indicate absolute abundance as we counted leeches that latched onto researchers walking transects. Therefore, our counts are reflective of active feeding behaviour. There are several means by which our occurrence may differ from actual leech abundance. For instance, leeches may remain dormant in particular

conditions, e.g., Fogden & Proctor (1985) noted that following a blood meal leeches exhibited a period of dormancy or sluggishness when they did not respond to host proximity. Additionally, both the species and sizes of the leech can influence ambush site preferences (Gąsiorek & Różycka, 2017; Miler et al., 2019) and thus the two species may have been disparately likely to latch onto researchers and thus be counted. This potential confound may make the two species' counts not directly comparable and therefore we modelled the two species' occurrences separately. A third limitation is that we only counted leeches along trails which could result in biases that we are not able to account for in our analysis. For example, Gąsiorek & Różycka (2017) noted that tiger leeches aggregated closer to trails than off-trail locations (Gąsiorek & Różycka, 2017) when compared to brown leeches (*H. subagilis*).

Our research highlights several gaps in knowledge of leech ecology that we suggest as foci for future research. While several past studies (e.g., Kendall, 2012, Drinkwater et al., 2019) have investigated leeches across a gradient of degradation, ranging from primary to logged forests to oil-palm plantations, ours is the only study that investigates leech ecology across natural gradients within undisturbed habitats. More data, however, are needed to further clarify the relationship between leeches and forest-dwelling vertebrates (i.e., their prey) when vertebrate densities are relatively unaffected by human factors. Additionally, investigations of variation across spatial and temporal axes would enrich our understanding of their potential as indicator species for arboreal, as well as crepuscular and nocturnal, vertebrates.

5. TABLES

Table 1: Total distance sampled on each sampling occasion and for the entire study duration within each forest type (MO – montane, UG – upland granite, LG – lowland granite, LS – lowland sandstone, AB – alluvial bench, FS – freshwater swamp, PS – peat swamp)

Forest Type	Altitude (m a.s.l.)	Distance (km) per sampling occasion	Total sampling distance (km)
MO	750-1100	3.8	702.0
UG	350-800	10.1	1766.6
LG	200-400	6.2	1235.6
LS	20-200	5.4	996.4
AB	5-50	5.5	1014.3
FS	5-10	4.3	788.8
PS	5-10	6.8	1245
			7748.7

6. **FIGURE LEGENDS**

Figure 1. Focal leech species (a) tiger leech, *Haemadipsa picta* (photograph credit: Charles J. Sharp, CC BY-SA 4.0 <https://creativecommons.org/licenses/by-sa/4.0>, via Wikimedia Commons) (b) brown leech (photograph credit: Alpsdake, CC BY-SA 3.0 <https://creativecommons.org/licenses/by-sa/3.0>, via Wikimedia Commons)

Figure 2. Map of the trail system at the Cabang Panti Research Site, Gunung Palung National Park, West Kalimantan, Indonesian Borneo. The inset box shows the location of the national park on the Island of Borneo. The coloured and dashed lines indicate the census routes along which leech data were collected.

Figure 3. Back-transformed (exponentiated) beta coefficients from the top model showing the odds of counting (a) the tiger leech and (b) the brown leech in response to abiotic (soil moisture & rain histories) and biotic (forest type & occurrence of other leech species) predictors.

Figure 4. Scatter plot showing variation in counts of the tiger leech and the brown leech across different forest types (MO – montane, UG – upland granite, LG – lowland granite, LS – lowland sandstone, AB – alluvial bench, FS – freshwater swamp, PS – peat swamp)
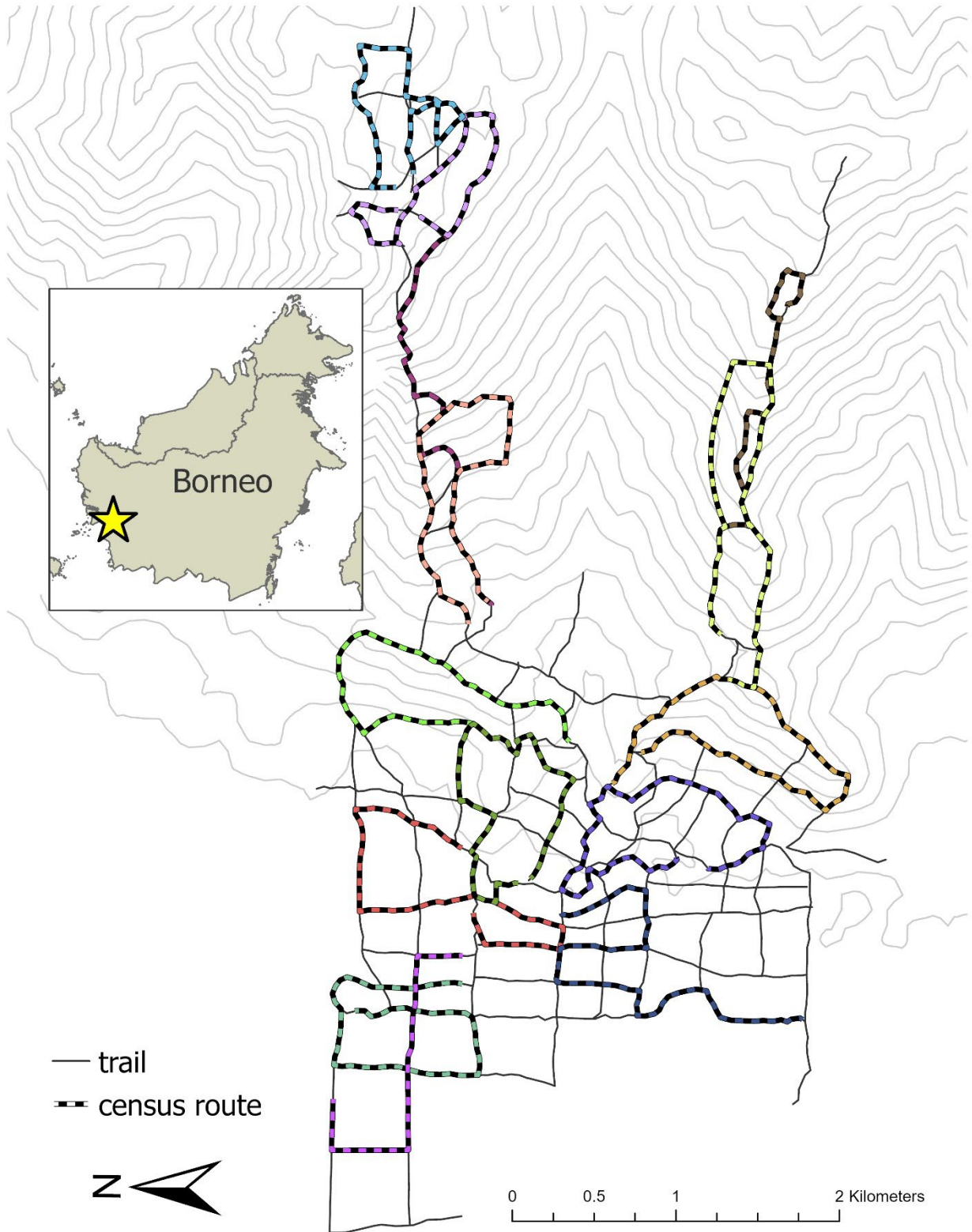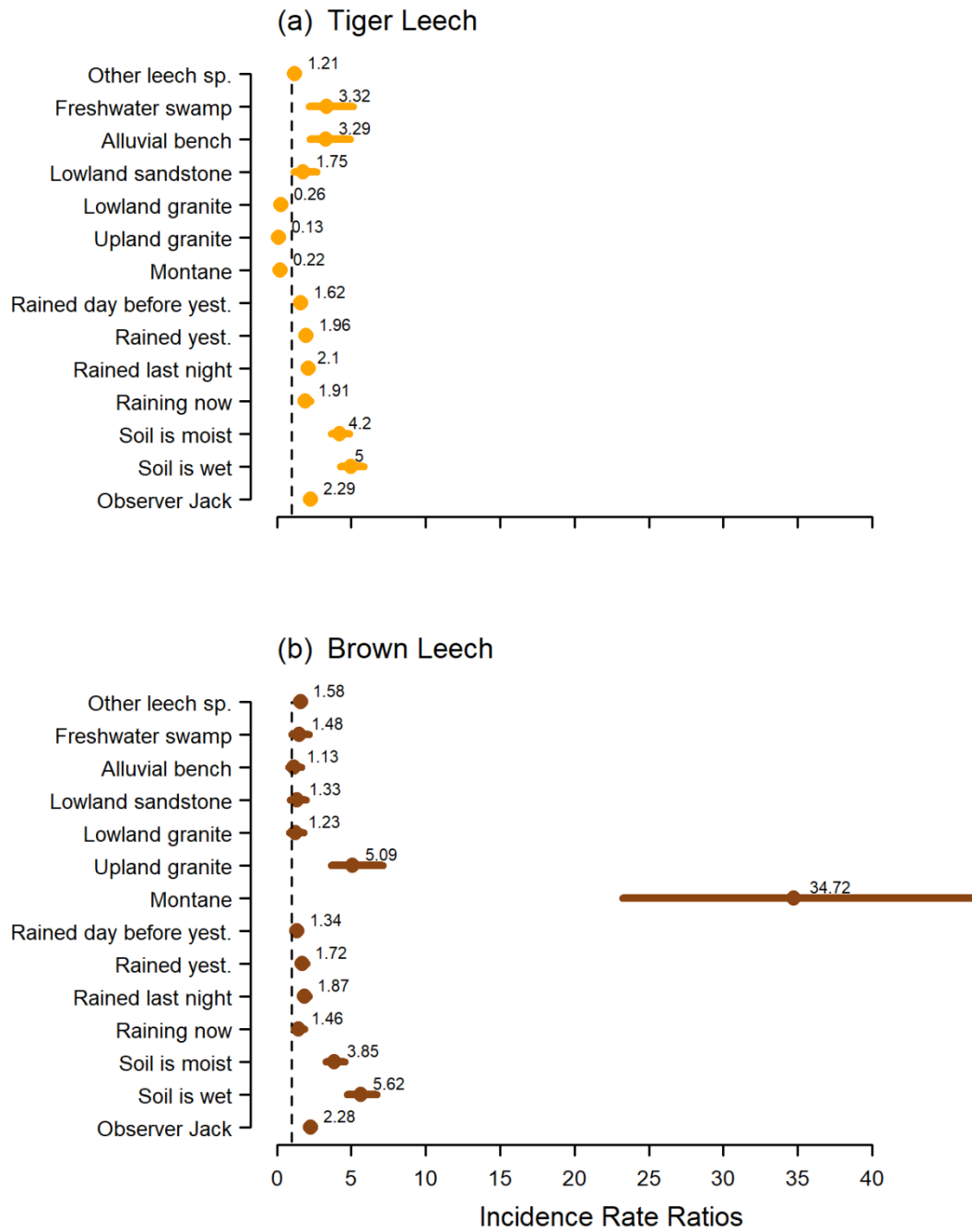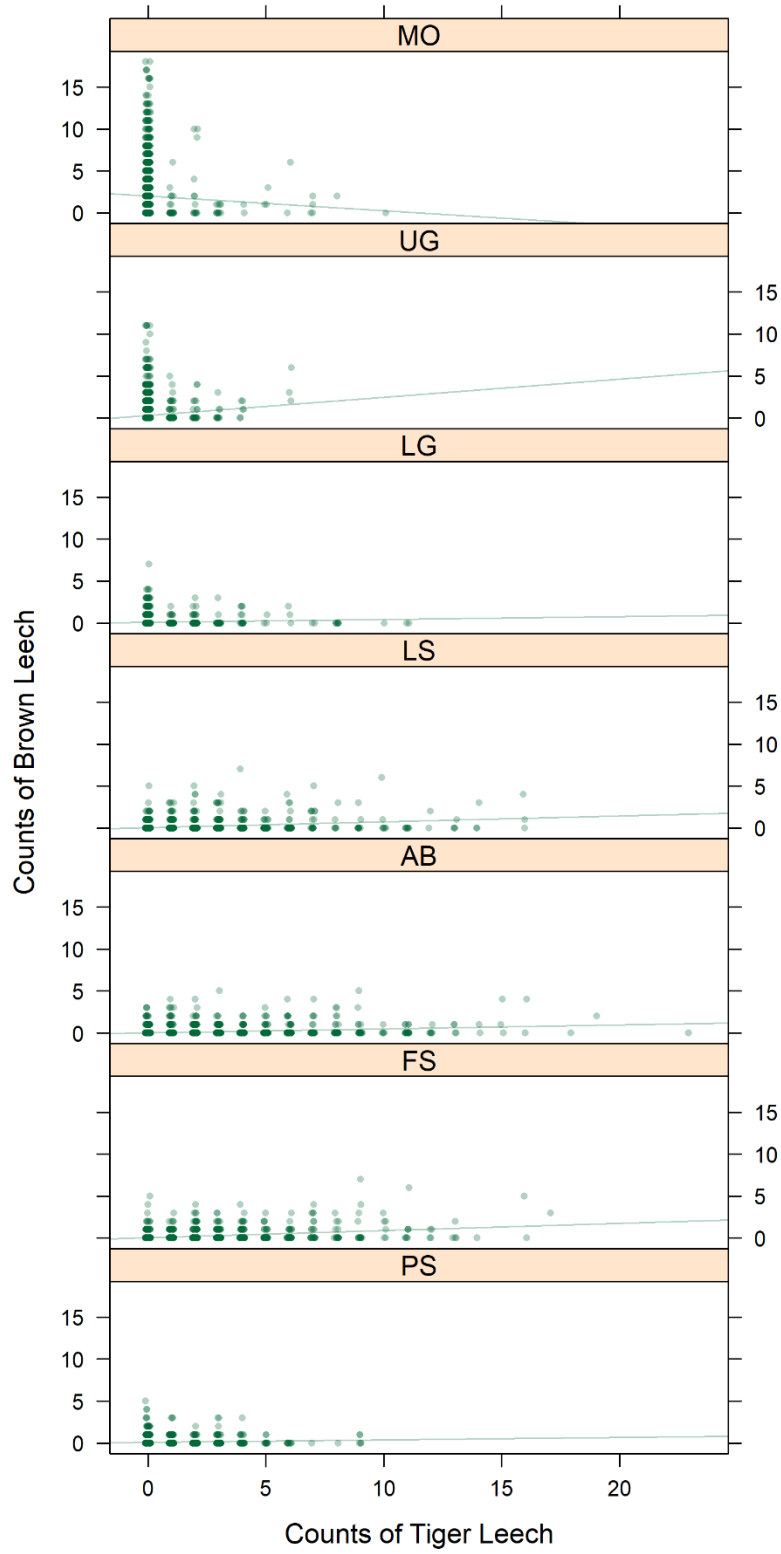
7. FIGURES

Figure 1.

(a)

(b)

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Figure 2.

Borneo

trail
census route

N   0   0.5   1   2 Kilometers

Figure 3.

(a) Tiger Leech

(b) Brown Leech

Incidence Rate Ratios

Figure 4.

MO

UG

LG

LS

AB

FS

PS

Counts of Brown Leech

Counts of Tiger Leech

8. ACKNOWLEDGEMENTS

Author Contribution Statement

AJM conceptualized the study. AJM and HUW acquired funding. AJM, ES, TWS, and TMS administered the project. AJM, RR, S, J, DA, SL, SMJ, EJB and ZJ conducted the field investigation. SL, SMJ, EJB and ZJ curated the data. SN, ABB, GRE, BJF and AJM conducted the formal analysis. SN, ABB, GRE, BJF, HUW and AJM wrote the original manuscript draft. All authors reviewed and edited the manuscript.

9. DISCLOSURE STATEMENTS

Conflict of Interest

No potential conflict of interest was reported by the authors

Ethical Guidelines

All applicable institutional and/or national guidelines for the care and use of animals were followed. Fieldwork was conducted under the approval of the Ministry of Research and Technology of the Republic of Indonesia, Jakarta, Indonesia and Balai Taman Nasional Gunung Palung, Ketapang, Kalimantan Barat, Indonesia.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.r4xgxd2g9 (Nelaballi *et al.* 2022), and https://github.com/andrewjohnmarshall/leech_distribution.

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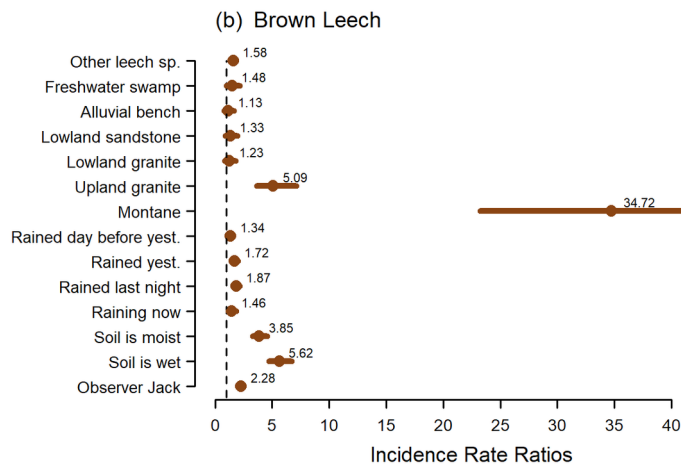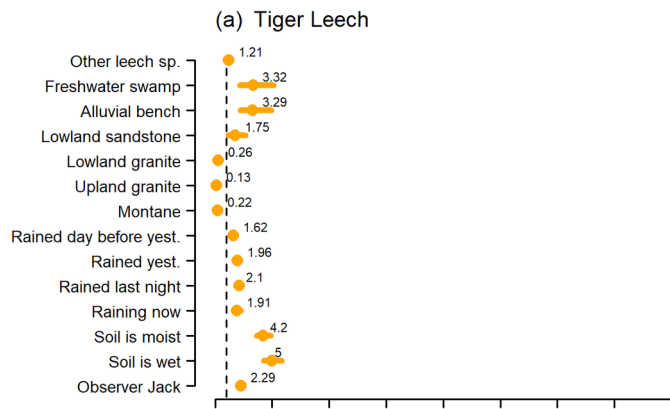
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(a) Tiger Leech

(b) Brown Leech

Incidence Rate Ratios

BTP_13146_BITR-22-052_Fig3.tiff

BTP_13146_BITR-22-052_Fig4.tiff